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Water-carbon coupling modeling of summer maize at the leaf and canopy scales

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Transpiration and photosynthesis are two closely related and intercoupled processes that dominate the physiological activities and yield of crops. Therefore, there is a need to study water-carbon coupling modeling at various scales to increase water use efficiency (WUE). Using a summer maize field in North China as an example, the variations in leaf and canopy photosynthesis and transpiration (or evapotranspiration) were analyzed. The synthetic model of photosynthesis-transpiration based on stomatal behavior (SMPT-SB) was then calibrated and validated at the two scales. The leaf photosynthesis and transpiration, as well as the canopy photosynthesis and evapotranspiration, have a consistent diurnal trend. However, the canopy evapotranspiration is affected more by topsoil moisture content. The regression coefficient between leaf photosynthesis, transpiration, and WUE estimated by the SMPT-SB and the measured values was found to approach 1, with a coefficient of determination of more than 0.74. The relative error between the two sets of values is less than 11%. Therefore, the SMPT-SB could express fairly well leaf photosynthesis, transpiration, and WUE. The estimated canopy-scale photosynthesis by the SMPT-SB is also in good agreement with the measured values. However, this model underestimates the canopy evapotranspiration when the topsoil has high moisture content and therefore overestimates, to a certain extent, the canopy WUE.

photosynthesis, transpiration, water use efficiency, SMPT-SB, stomatal conductance, maize

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Farmland water cycle and carbon cycle are closely related and intercoupled ecological processes that affect the physiological activities and yield of plants [1,2]. Hence, the coupling of water and carbon cycles should be studied to improve water use efficiency (WUE). And the study of water-carbon coupling at the leaf and canopy scales could provide an insight into the physio-ecological mechanism of stomatal control during water and carbon cycle processes, reveal the scale effect and intrinsic link of water-carbon coupling and serve as a basis in establishing a coordinated and unified water-carbon coupling model and WUE estimation method.

At present, evapotranspiration estimation models, including the Penman-Monteith (P-M) model [3,4], Shuttleworth-Wallace model [5], and other multilayer models [6,7], are mainly based on both energy and water equilibrium principles. Numerous plant photosynthesis models were also reported, such as the leaf biochemical model suggested by Farquar and Von Caemmerer in 1982, which expresses the photosynthetic rate as a function of intercellular carbon dioxide (CO_2) concentration, light quantum flux density, and temperature [8]. And the model is extensively used because of its few parameters [9–11]. Canopy-scale photosynthesis models are generally developed by expanding leaf photosynthesis models at the canopy scale, and they can be categorized into single-layer model [12,13], two-layer mod-

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el [14], and multilayer model [15].

Numerous observation tests indicate that leaf photosynthesis and transpiration show homoplasy with respect to various environmental factors. And the role of stomata in regulating vapor and CO_2 exchange between plants and the atmosphere has been identified and confirmed. However, the relationship between water and carbon fluxes is not a simple linear relation. Although stomata are the major channels of transpiration and photosynthesis, they have a slightly different response to these two processes. For instance, at a given transpiration amount, leaves regulate stomata initiatively to maximize the photosynthetic rate [16–18]. Thus, Leuning [18] and Collatz et al. [19] introduced the idea of coupling photosynthesis, transpiration, and heat balance. Ball developed a coupling model [20,21] of leaf stomatal conductance, net photosynthesis rate, and environmental factors, which has been widely applied at the leaf, canopy, water basin, and global scales [22–24]. Yu and Wang constructed a complete physiological model [25] consisting of leaf photosynthesis, transpiration, and stomatal conductance sub-models by considering boundary layer conductance. Moreover, large-scale water-carbon coupling models primarily include FOREST-BGC [26], AVIM [27], SiB2 [28], IBIS [29], and BEPS [30,31].

These models provide substantial information on the coupling mechanism of photosynthesis and transpiration. However, their complexity limits their extensive applications. Hence, Yu et al. [32,34] introduced CO_2 internal conductance based on the physiological mechanism of photosynthesis and transpiration controlled by stomatal behavior, and developed a synthetic model of photosynthesis-transpiration (SMPT-SB) [32,33]. The SMPT-SB was found to be useful in maize, soybean, and tree leaf scales. Ren et al. [35] also constructed canopy-scale SMPT-SB of broad-leaved forest in Changbai Mountain and revealed good results. However, the simultaneous application of this model at the leaf and canopy scales has not been reported.

Several studies on water and carbon fluxes have been carried out. However, a joint analysis of multi-scale water-carbon coupling relation [2,36] is rarely conducted. Therefore, the present study aims to analyze the variations of photosynthesis and transpiration (or evapotranspiration) rates at the leaf and canopy scales, calibrate and validate the water-carbon coupling SMPT-SB, and estimate the WUE. It also aims to analyze the model's influencing factors.

1 Water-carbon coupling SMPT-SB

1.1 Water-carbon coupling model at the leaf scale

(i) Transpiration model. Leaf water (H_2O) flux is a function of the atmosphere, plant, and other factors described below [33]:

$$T_{-L}=\frac{W_{i-L}-W_{a-L}}{1/g_{bw-L}+1/g_{sw-L}}, \tag{1}$$

where T_{-L} is the leaf transpiration rate, mmol m^{-2} s^{-1}; W_{i-L} and W_{a-L} are the mole fraction of water vapor in leaf stomata and in the atmosphere, respectively, mmol mol^{-1}; and g_{bw-L} and g_{sw-L} are the conductance to H_2O diffusion through the leaf boundary layer and leaf stomata, respectively, mol m^{-2} s^{-1}.

The stomatal conductance is estimated by the Ball model developed by Leuning et al. [33,37]:

$$g_{sw-L}=g_{0-L}+a_{1-L}A_{-L}RH_{-L}/(C_{s-L}-\Gamma_{-L}), \tag{2}$$

where A_{-L} is the leaf photosynthetic rate, μmol m^{-2} s^{-1}; g_{0-L} is the residual stomatal conductance (as $A_{-L}\rightarrow 0$ when light quantum flux density $\rightarrow 0$), mol m^{-2} s^{-1}; C_{s-L} is the ambient CO_2 concentration at the leaf surface, μmol m^{-2} s^{-1}; Γ_{-L} is the CO_2 compensation point with dark respiration, μmol m^{-2} s^{-1}; RH_{-L} is the relative humidity at the leaf surface; and a_{1-L} is a coefficient.

(ii) Photosynthesis model. Considering the effect of biochemical and photochemical processes in the boundary layer, stoma, and mesophyll, then the photosynthesis rate model may be expressed as follows [33]:

$$A_{-L}=\frac{C_{a-L}-\Gamma_{*-L}}{1/g_{bc-L}+1/g_{sc-L}+1/g_{ic-L}}, \tag{3}$$

where C_{a-L} is the ambient CO_2 concentration, μmol mol^{-1}; Γ_{*-L} is the CO_2 compensation point without dark respiration, μmol mol^{-1}; g_{bc-L} and g_{sc-L} are the conductance of the leaf boundary layer and leaf stomata to CO_2, respectively, mol m^{-2} s^{-1}; and g_{ic-L} is the leaf "internal" conductance, mol m^{-2} s^{-1}.

Yu et al. [33] stated that the "internal" conductance may be expressed by the following formula without any environmental stress:

$$g_{ic-L}=M+NQ_p, \tag{4}$$

where Q_p is the light quantum flux density, μmol m^{-2} s^{-1}; and M and N are coefficients.

(iii) Photosynthesis-transpiration coupling model. In the field experiment, Γ_{*-L} and Γ_{-L} are approximately equal, and g_{0-L} could generally be ignored when considering the diffusion of CO_2 through stomata. Assuming that $g_{sw-L}=1.56g_{sc-L}$ and $g_{bw-L}=1.37g_{bc-L}$, then the leaf photosynthesis and transpiration rates may be expressed as follows [33]:

$$A_{-L}=\frac{(C_{a-L}-\Gamma_{*-L})[1-1.56/(a_{1-L}RH_{-L})]}{1.37/g_{bw-L}+1/g_{ic-L}}, \tag{5}$$

$$T_{-L}=\frac{W_{i-L}-W_{a-L}}{\dfrac{1}{g_{bw-L}}+\dfrac{1}{g_{0-L}+\dfrac{(a_{1-L}RH_{-L}-1.56)}{(1.37/g_{bw-L}+1/g_{ic-L})}}}. \tag{6}$$

(iv) WUE model. With eqs. (5) and (6) simultaneously in place, the WUE model can be derived as follows:

$$\mathrm{WUE}_{-L}=\frac{A_{-L}}{T_{-L}}=\frac{(C_{a-L}-\Gamma_{*-L})\left[1-\dfrac{1.56}{(a_{1-L}RH_{-L})}\right]}{W_{i-L}-W_{a-L}}K_{r\text{-}L}, \quad (7)$$

$$K_{r-L}=\frac{1/g_{bw-L}}{1.37/g_{bw-L}+1/g_{ic-L}}+\frac{1}{g_{0-L}\left(\dfrac{1.37}{g_{bw-L}}+\dfrac{1}{g_{ic-L}}\right)+a_{1-L}RH_{-L}-1.56}, \quad (8)$$

where WUE_{-L} is the WUE at the leaf scale, μmol mmol^{-1}.

1.2 Water-carbon coupling model at the canopy scale

When the leaf area index (LAI) is more than 3, the CO_2 rate of the water-carbon coupling model at the canopy scale can be estimated using the following formula [35]:

$$A_{-C}=\frac{(C_{r-C}-\Gamma_{*-C})[1-1.56/(a_{1-C}RH_{-C})]}{1.37/g_{bw-C}+1/g_{ic-C}+1/g_{a-C}}, \quad (9)$$

where A_{-C} is the photosynthetic rate at the canopy scale, μmol $\mathrm{m}^{-2}\ \mathrm{s}^{-1}$; C_{r-C} is the CO_2 concentration in the atmosphere at the reference height, μmol mol^{-1}; Γ_{*-C} is the CO_2 compensation point of a virtual leaf without dark respiration, μmol mol^{-1}; g_{bw-C} is the conductance to H_2O diffusion through the virtual leaf boundary layer at the canopy scale, mol $\mathrm{m}^{-2}\ \mathrm{s}^{-1}$; g_{ic-C} is the "internal" conductance of the virtual leaf, mol $\mathrm{m}^{-2}\ \mathrm{s}^{-1}$; g_{a-C} is the aerodynamic conductance, mol $\mathrm{m}^{-2}\ \mathrm{s}^{-1}$; RH_{-C} is the relative humidity of the air around the virtual leaf; and a_{1-C} is a coefficient.

The transpiration rate at the canopy scale can be expressed as follows:

$$ET_{-C}=\frac{W_{i-C}-W_{r-C}}{\dfrac{1}{g_{a-C}}+\dfrac{1}{g_{bw-C}}+\dfrac{1}{g_{0-C}+\dfrac{a_{1-C}RH_{-C}-1.56}{\dfrac{1.37}{g_{bw-C}}+\dfrac{1}{g_{ic-C}}+\dfrac{1}{g_{a-C}}}}}, \quad (10)$$

where ET_{-C} is the evapotranspiration rate at the canopy scale, mmol $\mathrm{m}^{-2}\ \mathrm{s}^{-1}$; W_{i-C} and W_{r-C} are the mole fraction of water vapor in the virtual leaf stomata and in the atmosphere at the reference height, respectively, mmol mol^{-1}; and g_{0-L} is the residual stomatal conductance of the virtual leaf (as $A_{-C}\rightarrow 0$ when light quantum flux density $\rightarrow 0$), mol $\mathrm{m}^{-2}\ \mathrm{s}^{-1}$.

The "internal" conductance at the canopy scale is the integral of light quantum flux density over the canopy:

$$g_{ic-C}=\int_{Q_b}^{Q_t}(M+NQ_p)=MQ_t(1-\mathrm{e}^{-\varepsilon LAI})+\frac{1}{2}NQ_t^2(1-\mathrm{e}^{-2\varepsilon LAI}), \quad (11)$$

where Q_t and Q_b are the light quantum flux densities at the top and bottom of the canopy, respectively, μmol $\mathrm{m}^{-2}\ \mathrm{s}^{-1}$; ε is the coefficient of extinction; and LAI is the leaf area index.

With eqs. (9) and (10) simultaneously in place, the WUE at the canopy scale was derived using the following formula:

$$WUE_{-C}=\frac{A_{-C}}{ET_{-C}}=\frac{(C_{r-C}-\Gamma_{*-C})\left[1-\dfrac{1.56}{(a_{1-C}RH_{-C})}\right]}{W_{i-C}-W_{r-C}}K_{r\text{-}C}, \quad (12)$$

$$K_{r-C}=\frac{1/g_{a-C}+1/g_{bw-C}}{1.37/g_{bw-C}+1/g_{ic-C}+1/g_{a-C}}+\frac{1}{g_{0-C}\left(\dfrac{1.37}{g_{bw-C}}+\dfrac{1}{g_{ic-C}}+\dfrac{1}{g_{a-C}}\right)+a_{1-C}RH_{-C}-1.56}, \quad (13)$$

where WUE_{-C} is the WUE at the canopy scale, μmol mmol^{-1}. Other model parameters can be found in [33,35].

1.3 Model evaluation indices

The effect of the model is primarily evaluated using the coefficient of regression (b), the coefficient of determination (R^2), root-mean-square error (RMSE), mean absolute error (MAE), coefficient of consistency (d_{IA}), and mean. Their calculation can be found in the literature [38].

2 Materials and methods

2.1 Experimental site

The field experiment was conducted during the growth stage of summer maize from 2008 to 2010 (June to October) at the Irrigation Experiment Station, Institute of Water Resources and Hydropower Research (IWHR), Beijing, China (39°37′N 116°26′E; elevation of 40.1 m). The station is located in a semi-arid to sub-humid climate zone, with a mean annual sunshine duration of 2600 h, a mean annual temperature of 12.1°C, an annual accumulated temperature (>10°C) of 4730°C, a mean frost-free period of 185 d, a mean annual precipitation of 540 mm, and a mean annual evaporation from a free water surface of 1800 mm. The area is dominated by sandy loam.

Xuenuo No.2 species is planted during the summer of 2008–2010. The seeding time, harvest time, entire development stage, and rainfall amount are listed in Table 1, while the irrigation schedule is shown in Table 2.

2.2 Measurements

(i) Photosynthesis, transpiration, and stomatal conductance at the leaf scale. During the maize development stage in

Table 1 Seeding time, harvest time, entire development stage, and rainfall amount

Year	Seeding time	Harvest time	Development state (d)	Rainfall during the development stage (mm)
2008	June 25	October 6	104	307.2
2009	June 16	October 2	109	344.8
2010	June 25	October 6	104	258.8

Table 2 Irrigation schedule during the entire development stage of summer maize (including pre-sowing irrigation)

Year	Irrigation date	Irrigation quantity (mm)	Year	Irrigation date	Irrigation quantity (mm)
2008	June 22	45	2010	June 23	30
	July 29	40		July 24	72
	September 4	40		August 11	70
2009	June 30	40			

2008–2009, the diurnal variations in leaf photosynthesis (A_{-L}), transpiration (T_{-L}), stomatal conductance (g_{sw-L}), photosynthetically active radiation (PAR), temperature, and humidity were measured every 10–15 d using Li-6400 (Li-COR, USA). Five and six measurements were made in 2008 and 2009, respectively. Hourly readings were taken from 08:00 to 16:00. For each measurement, eight representatives of maize plants were randomly selected, wherein three functional leaves (one each from the top, middle, and bottom) were selected for measurement. The measurement point was the center of the leaves, which were held constantly perpendicular to the sunshine during measurement. A total of 24 leaves were used in each operation to measure A_{-L}, T_{-L}, g_{sw-L}, and other relevant environmental factors.

In 2010, the diurnal variations in the A_{-L}, T_{-L}, and g_{sw-L} of the leaves in their natural state, as well as temperature and humidity, were measured on five occasions, each continued from 08:00 to 16:00 with 2 h intervals. During each measurement, two representatives of maize plants were randomly selected, wherein six functional leaves (two each from the top, middle, and bottom) were selected. The measurement point was the center of the leaves. A total of 12 representative leaves in their natural state were measured for their A_{-L}, T_{-L}, and g_{sw-L}, and other relevant environmental factors.

(ii) Photosynthesis and evapotranspiration at the canopy scale. Canopy-scale photosynthesis and evapotranspiration rates were measured using the eddy covariance system (Campbell Scientific Inc., USA):

$$F_{-C}=\frac{10^6}{44}\overline{w'\rho_c'}, \tag{14}$$

$$\lambda ET_{-C}=\lambda\rho_a\overline{w'q'}, \tag{15}$$

where F_{-C} is the canopy CO_2 flux, μmol m^{-2} s^{-1}; λET_{-C} is the latent heat flux, W m^{-2}; ρ_a is the air density, kg m^{-3}; w' is the pulsating quantity of vertical wind speed, m s^{-1}; ρ_c' is the CO_2 density, g m^{-3}; q' is the pulsating quantity of vapor density, g m^{-3}; and $10^6/44$ is the conversion factor of unit.

The eddy covariance system used in the present study consists of a 3D sonic anemometer/thermometer (model CSAT3), a CO_2/H_2O open-circuit gas analyzer (model LI-7500), a temperature and humidity sensor (model HMP45C), a net radiometer (model NR01), two heat flux plates (model HFP01), and a CR5000 data collector (Campbell Scientific Inc., USA). The 3D sonic anemometer/thermometer and the CO_2/H_2O open-circuit gas analyzer were used to measure the vertical fluctuations of wind and the CO_2/H_2O density at 0.1 s intervals, respectively. These sensors were mounted at 3.1 m above the ground. The net radiometer mounted at 4 m above the ground was used to measure the mean net radiation for 30 min periods. The ground heat flux (G) was measured using soil heat flux plates installed at 20 mm depth below the soil, and data were averaged over 30 min periods. All sensors were connected to a data logger (model CR5000, Campbell Scientific Inc., Logan, UT, USA), and statistical analysis (average, variance, and covariance) was conducted for 30 min periods. Measurements were made from 2008 to 2010. During eddy covariance data processing, the outliers that were removed are described as follows: (1) data during precipitation period and 1 h before and after precipitation; (2) data apparently exceeding the physical meaning; and (3) data measured when the sensor was malfunctioning. Moreover, the Bowen ratio was computed to correct the latent heat flux, which was used to remove errors due to energy miscalculation [39].

(iii) Virtual leaf stomatal conductance at the canopy scale. Using the eddy covariance method to measure the canopy-scale latent heat flux, the P-M formula was used to derive reversely the virtual leaf stomatal conductance g_{sw-C} at the canopy scale:

$$g_{sw-C}=\frac{100}{2.24}\times\left[\frac{\gamma\cdot\lambda ET_{-C}\cdot(2.24/100\cdot g_{a-C})}{\Delta(R_n-G)+\rho_a C_p \mathrm{VPD}\cdot g_{a-C}-(\Delta+\gamma)\cdot\lambda ET_{-C}}\right]-g_{bw-C}, \tag{16}$$

where R_n is the net radiation, W m^{-2}; G is the soil heat flux, W m^{-2}; VPD is the saturation deficit, kPa; γ is the hygrograph constant, kPa °C^{-1}; Δ is the slope of saturated vapor-temperature curve, kPa °C^{-1}; and C_p is the constant pressure specific heat of air, J kg^{-1} K^{-1}.

(iv) Other parameters. The LAI was measured once every 5 d, and 51 representative plants were selected each time. The length and width of their leaves were measured, and the leaf area of each maize plant was calculated, then the LAI could be derived according to the planting density.

The coefficient of extinction ε was measured using the SunScan canopy analysis system (Dynamax, Inc., USA). Measurements were made every 5 d, with each measurement consisting of 45 measurement points. The PAR was measured continuously from 10:00 to 12:00 at the top and bottom of the canopy, and the mean values were calculated. The coefficient of extinction was computed from the measured LAI [40].

Canopy temperature was measured using a portable IR thermometer. Each measurement consisted of 120 randomly selected measurement points, and their mean value was used as the canopy temperature.

Meteorological factors such as precipitation, humidity, and wind speed were measured using an automatic weather station (Monitor Sensors, Australia). A set of meteorological data was recorded automatically every 30 min.

3 Results and discussion

3.1 Diurnal variation of photosynthesis and transpiration at the leaf and canopy scales

Figure 1 shows the diurnal variation of the photosynthesis, transpiration, and PAR of summer maize leaves in their natural state at different canopy heights on two typical days in 2010 (August 5 and 15; the plant height was 1.1 and 1.8 m, respectively, and the LAI was 2.5 and 3.7, respectively). As shown in Figure 1, A_{-L} and T_{-L} at different heights of the canopy increased and reached their peaks (at around 12:00) when the PAR increased, and then decreased when the PAR

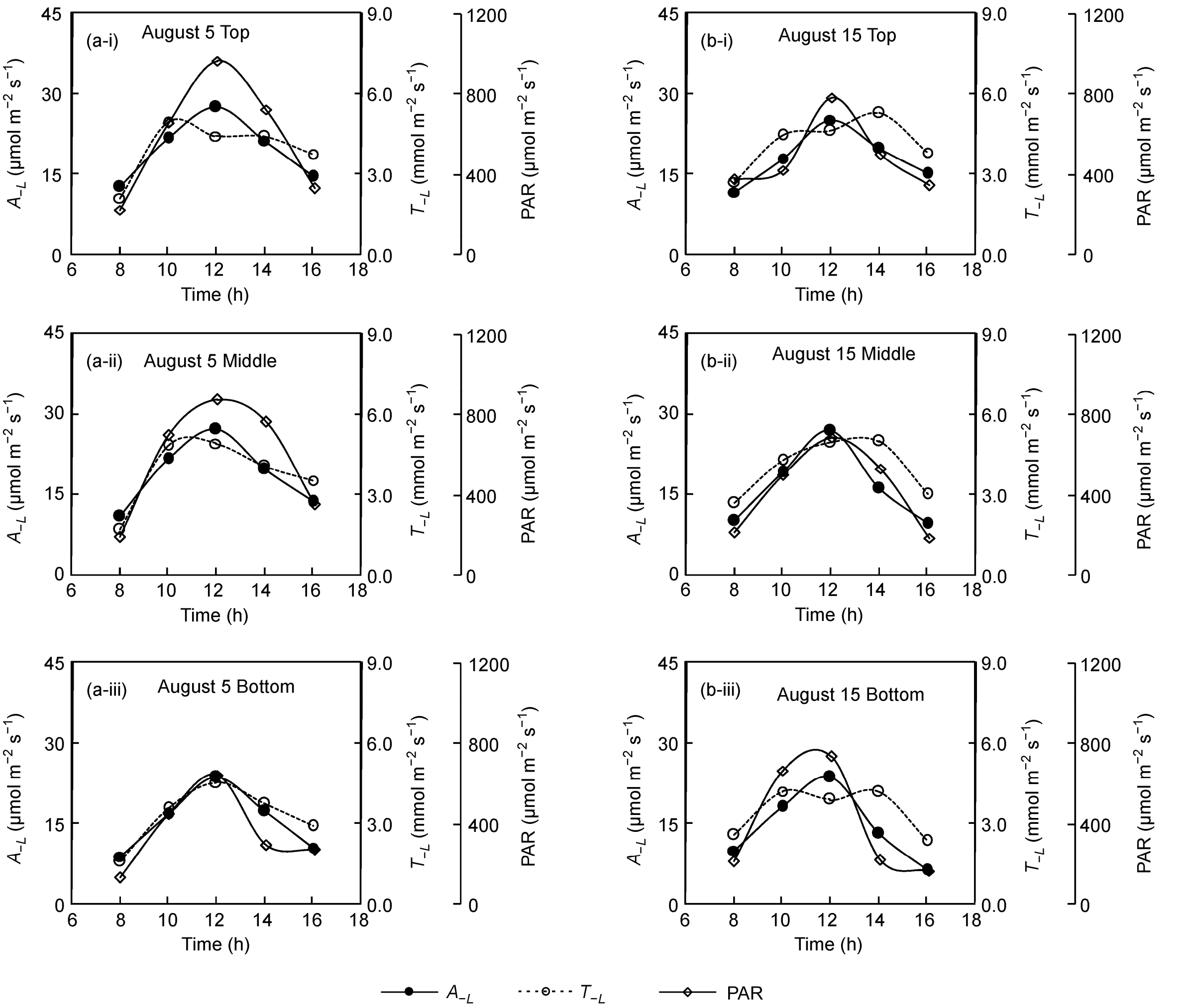

Figure 1 Diurnal variation of photosynthesis, transpiration, and PAR of leaves in their natural state at different canopy heights on typical days during the development stage of summer maize in 2010.

diminished. In addition, the photosynthesis and transpiration of leaves at the lower part of the canopy were less than those of leaves at the middle and upper parts of the canopy. This finding may be attributed to leaf age difference. Overall, the diurnal variation of the photosynthesis and transpiration of leaves at different heights of the canopy is consistent.

As shown in Figure 2, the diurnal variation of net photosynthesis rate and evapotranspiraton at the canopy scale is also substantially consistent. Furthermore, the photosynthesis rate differed less on these 2 d, but their evapotranspiration greatly varied. This finding may be explained by the large difference in topsoil moisture content between these 2 d because of an irrigation made on August 11 and several precipitations recorded therein. On August 3, the root zone soil moisture accounted for 70% of field capacity moisture, and the average moisture of the top 10 cm soil accounted for 63% of field capacity moisture. On August 15, the root zone soil moisture accounted for 80% of field capacity moisture, and the moisture of the top 10 cm soil accounted for 85% of field capacity moisture.

3.2 Analysis of the simulation results of the leaf-scale photosynthesis-transpiration coupling model

The leaf-scale water-carbon coupling model was calibrated using the data measured on typical growth stage days (leaf photosynthesis measurement dates) of summer maize in 2008. This model was validated using the measurement data of 2009 and 2010 (Figures 3 and 4; Table 3). As shown in Figure 3, the photosynthesis, transpiration, and WUE estimated by the model are substantially consistent with the diurnal variation trend of the measured values. As shown in Figure 4(a) and Table 3, when fitted to the measured data,

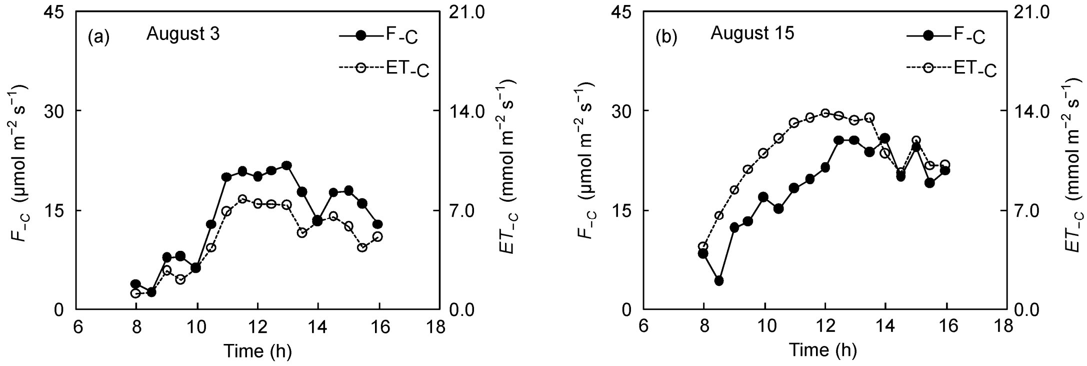

Figure 2 Diurnal variation of net photosynthetic rate and evapotranspiration at the canopy scale on typical days during the development stage of summer maize in 2010.

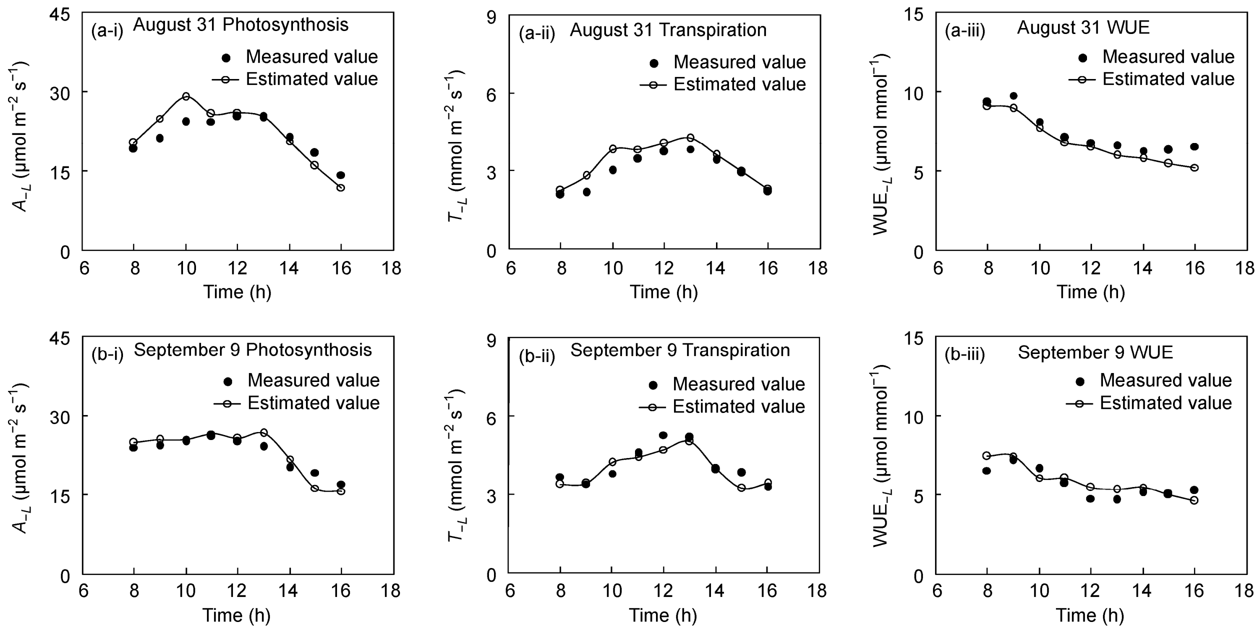

Figure 3 Diurnal variation of simulated and measured leaf photosynthesis, transpiration, and WUE values of summer maize during the development stage in 2009.

Table 3 Statistics of simulated and measured leaf-scale photosynthesis, transpiration, and WUE values of summer maize during the development stage in 2009 and 2010[a)]

Model	b	R^2	d_{IA}	RMSE	MAE	$\overline{O_{-L}}$	$\overline{P_{-L}}$
Photosynthesis	1.07	0.84	0.90	4.16 μmol m^{-2} s^{-1}	3.29 μmol m^{-2} s^{-1}	22.46 μmol m^{-2} s^{-1}	23.94 μmol m^{-2} s^{-1}
Transpiration	1.10	0.86	0.91	0.93 mmol m^{-2} s^{-1}	0.71 mmol m^{-2} s^{-1}	3.92 mmol m^{-2} s^{-1}	4.35 mmol m^{-2} s^{-1}
WUE	0.95	0.74	0.88	1.08 μmol mmol^{-1}	0.86 μmol mmol^{-1}	6.06 μmol mmol^{-1}	5.77 μmol mmol^{-1}

a) $\overline{O_{-L}}$ is the mean of measured leaf-scale values; $\overline{P_{-L}}$ is the mean of simulated leaf-scale values of the model.

the leaf photosynthesis estimated by the model gives a regression coefficient b of 1.07, R^2 of 0.84, d_{IA} of 0.90, RMSE of 4.16 μmol m^{-2} s^{-1}, and MAE of 3.29 μmol m^{-2} s^{-1}. The mean leaf photosynthesis estimated by the model and the measured value were 23.94 μmol m^{-2} s^{-1} and 22.46 μmol m^{-2} s^{-1}, respectively. These data indicate that the model fairly reflects the variation of the summer maize leaf photosynthesis in this region.

As shown in Figure 4(b) and Table 3, the model slightly overestimated the leaf transpiration when fitted to the measured data and provided b of 1.10, R^2 of 0.86, d_{IA} of 0.91, RMSE of 0.93 mmol m^{-2} s^{-1}, and MAE of 0.71 mmol m^{-2} s^{-1}. The leaf transpiration value estimated by the model and the measured value were 4.35 mmol m^{-2} s^{-1} and 3.92 mmol m^{-2} s^{-1}, respectively. The model also performed well in estimating the WUE, yielding b of 0.95, R^2 of 0.74, d_{IA} of 0.88, RMSE of 1.08 μmol mmol^{-1}, and MAE of 0.86 μmol mmol^{-1}.

In summary, this leaf-scale water-carbon coupling model, SMPT-SB, reflects fairly the coupling relation between leaf photosynthesis and transpiration, and reasonably predicts the leaf WUE variation. Yu et al. verified the leaf-scale SMPT-SB using the measured data of maize and soybean. They found that this model could well simulate the photosynthesis, transpiration, and WUE without any environmental stress, which is in agreement with our results. However, the simulated values still show some errors with the measured values because the effects of leaf location and age on the plants were not considered. And the soil moisture and nutrient may affect the model prediction [34].

3.3 Analysis of the simulation results of the canopy-scale photosynthesis-evapotranspiration coupling model

The canopy water-carbon coupling model was calibrated using the data measured on typical growth stage days (photosynthesis measurement dates with a summer maize LAI greater than 3) of summer maize in 2008. This model was validated using the measurement data of 2009 and 2010 (Figure 5 and Table 4). As shown in Figure 5(a) and Table 4,

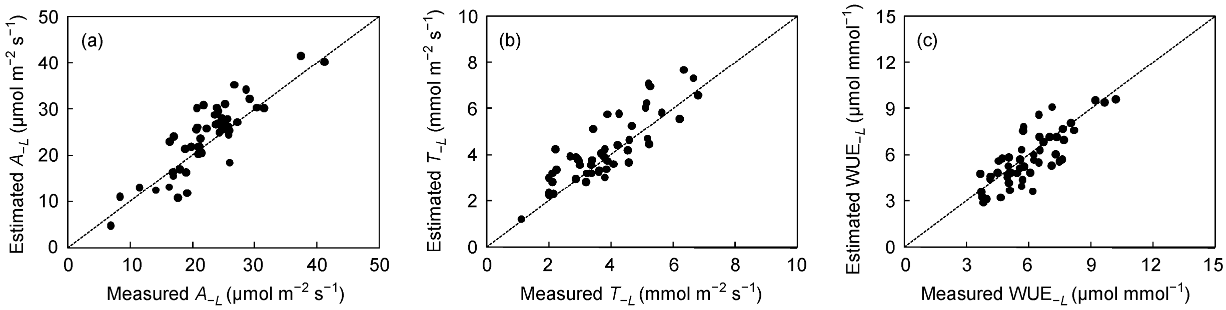

Figure 4 Comparison of simulated and measured leaf photosynthesis, transpiration, and WUE values of summer maize during the development stage in 2009 and 2010.

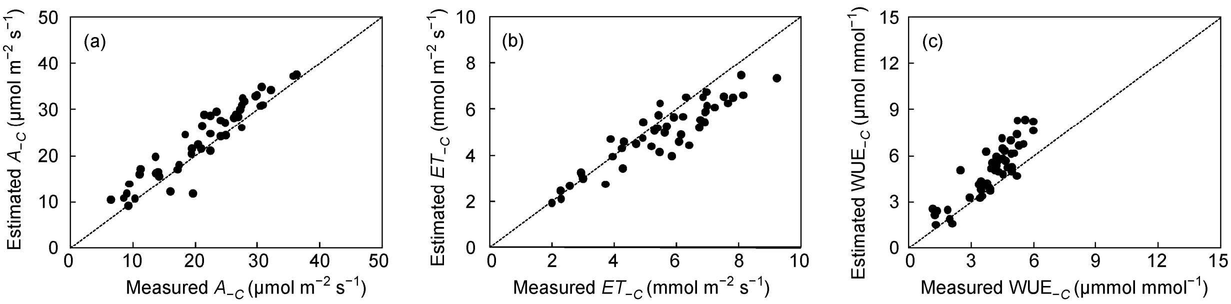

Figure 5 Comparison of simulated and measured canopy-scale photosynthesis, evapotranspiration, and WUE values of summer maize during the development stage in 2009 and 2010.

Table 4 Statistics of simulated and measured canopy-scale photosynthesis, evapotranspiration, and WUE values of summer maize during the development stage in 2009 and 2010[a)]

Model	b	R^2	d_{IA}	RMSE	MAE	$\overline{O_{-C}}$	$\overline{P_{-C}}$
Photosynthesis	1.08	0.88	0.93	3.38 μmol m^{-2} s^{-1}	2.70 μmol m^{-2} s^{-1}	21.52 μmol m^{-2} s^{-1}	23.49 μmol m^{-2} s^{-1}
Evapotranspiration	0.88	0.85	0.92	0.97 mmol m^{-2} s^{-1}	0.77 mmol m^{-2} s^{-1}	5.66 mmol m^{-2} s^{-1}	5.04 mmol m^{-2} s^{-1}
WUE	1.24	0.77	0.82	1.32 μmol $mmol^{-1}$	1.04 μmol $mmol^{-1}$	4.02 μmol $mmol^{-1}$	4.96 μmol $mmol^{-1}$

a) $\overline{O_{-C}}$ is the mean of measured canopy-scale values; $\overline{P_{-C}}$ is the mean of simulated canopy-scale values of the model.

when fitted to the measured values, the canopy-scale photosynthesis estimates of the model yielded b of 1.08, R^2 of 0.88, d_{IA} of 0.93, RMSE of 3.38 μmol m^{-2} s^{-1}, and MAE of 2.70 μmol m^{-2} s^{-1}. The mean canopy-scale photosynthesis value estimated by this model and the measured value were 23.49 μmol m^{-2} s^{-1} and 21.52 μmol m^{-2} s^{-1}, respectively. These data indicate that the model estimates fairly well the canopy-scale photosynthesis. Compared with the photosynthesis simulation, the simulation of canopy evapotranspiration has a slightly lower precision (Figure 5(b) and Table 4). The simulated canopy evapotranspiration and the measured values produced b of 0.88, R^2 of 0.85, d_{IA} of 0.92, RMSE of 0.97 mmol m^{-2} s^{-1}, and MAE of 0.77 mmol m^{-2} s^{-1}. The mean canopy evapotranspiration value predicted by the model and the measured value were 5.04 mmol m^{-2} s^{-1} and 5.66 mmol m^{-2} s^{-1}, respectively.

As shown in Figures 5(b), 6 and 7 and Table 4, the model underestimates evapotranspiration when the actual evapotranspiraion is large. This may be attributed to the fact that the single-layer model neglects soil evaporation, particularly when the topsoil contains large quantity of moisture (such as after a rain or irrigation). If soil evaporation accounts for a high proportion among the total evapotranspiration, the single-layer model's neglect for soil evaporation could reduce the precision of the canopy evapotranspiration simulation. Hence, the effect of soil moisture should be given emphasis in the further enhancement of the model. Ren et al. revealed that the percentage of soil evaporation in the total evapotranspiration greatly affects evapotranspiration simulation [35], which is consistent with our results. However, the photosynthesis rate at the canopy scale did not exhibit a significant difference despite the topsoil moisture difference because the root zone soil moisture was consistently large (data not given).

Based on Figure 5(c) and Table 4, the model overestimates the canopy-scale WUE because of the following main reasons. First, when the canopy evapotranspiration is less, a slight overestimation of photosynthesis or a slight underestimation of evapotranspiration results in a large overestimation of the WUE, an example of this is the WUE at 8:00 in Figure 6(a). Second, the model underestimates the canopy evapotranspiration but overestimates the photosynthesis, resulting in overestimated canopy WUE, an example is shown in Figure 6(b).

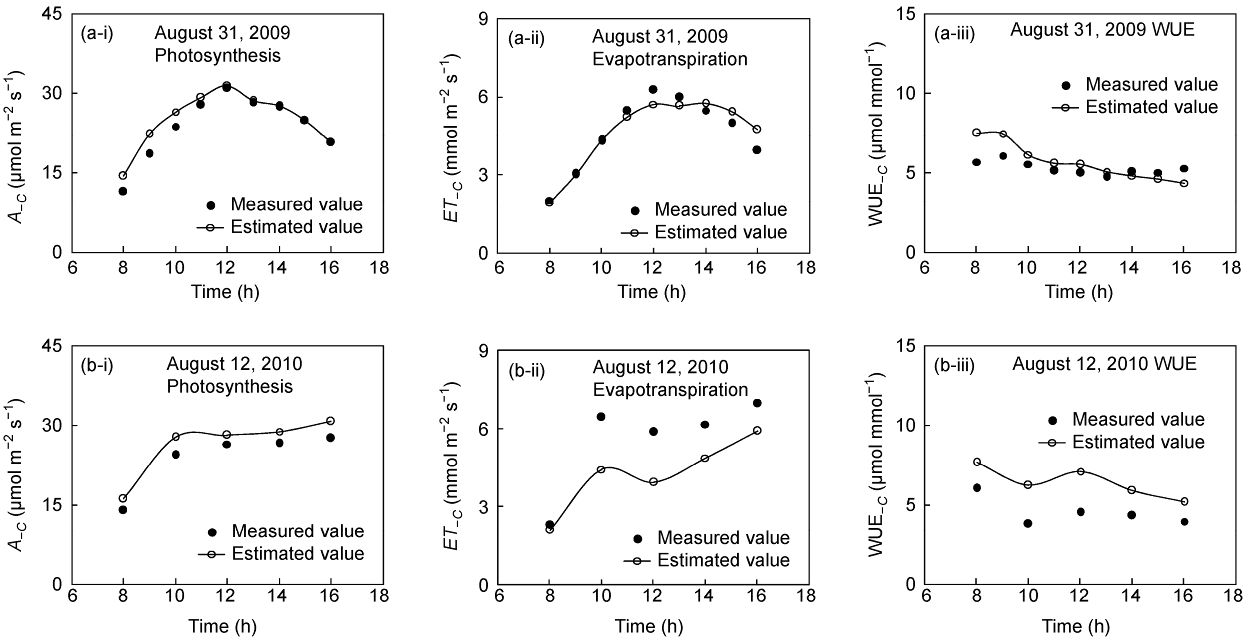

Figure 6 Diurnal variation of simulated and measured canopy-scale photosynthesis, evapotranspiration, and WUE values of summer maize during the development stage: topsoil moisture accounts for (a) 67% and (b) 90% of field capacity moisture.

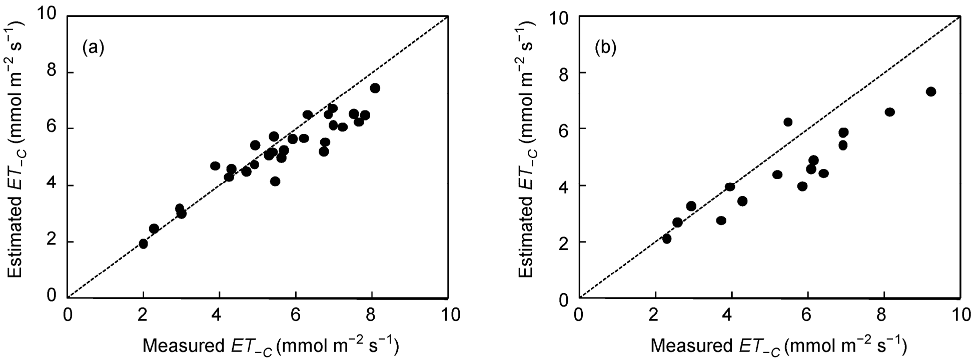

Figure 7 Comparison of simulated and measured canopy-scale evapotranspiration values with different topsoil moisture contents: topsoil moisture accounts for (a) less than 70% and (b) over 85% of field capacity moisture.

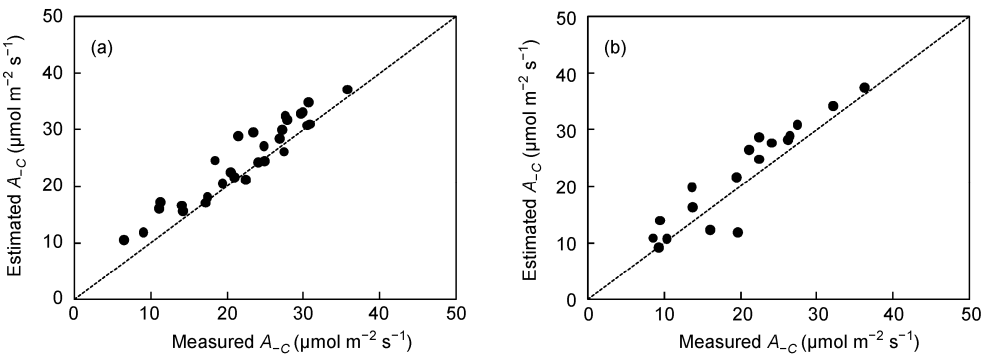

Figure 8 Comparison of simulated and measured canopy-scale photosynthesis values with different topsoil moisture contents: topsoil moisture accounts for (a) less than 70% and (b) over 85% of field capacity moisture.

4 Conclusion

The diurnal variations in the leaf and canopy photosynthesis and transpiration (or evapotranspiration) were systematically analyzed, and the SMPT-SB on these two scales were calibrated and validated. The major conclusions include the following:

(1) The diurnal variation of photosynthesis and transpiration (or evapotranspiration) is consistent at the leaf and canopy scales.

(2) The leaf photosynthesis, transpiration, and WUE estimated by the SMPT-SB are consistent with the measured values, fairly reflecting the SMPT-SB could well express the response of leaf photosynthesis, transpiration, and WUE to various environmental factors and the water-carbon coupling relationship.

(3) The SMPT-SB coupling model estimates the canopy-scale photosynthesis and shows good agreement with the measured values. However, this model underestimates the evapotranspiration when the topsoil contains high amount of moisture and overestimates, to a certain extent, the WUE.

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